DOES STANDARD METABOLIC RATE EXPLAIN PERSONALITY VARIATION IN EURASIAN PERCH (*PERCA FLUVIATILIS* L.)?

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Fishing-induced evolutionary changes in fish populations have been widely studied in recent years in the context of commercial as well as recreational fisheries. Because life histories have a genetic basis, the increased mortality caused by fishing shifts the age and size at reproduction towards younger and smaller, respectively. In addition, selective fishing for example by size or behaviour is likely to cause additional selection. Because personality traits have a genetic basis, the selectivity of recreational fishing for example through selective gear may be directed towards them as well. Consistent individual differences in behaviour have further been associated with life history traits, such as growth rate or reproductive success, in species across animal taxa. Therefore, fishing-induced selection on behavioural traits is of applied interest from the perspective of fisheries management as well. Because also the consistent individual differences in metabolism have been associated with differences in life history traits, the potential connection between metabolic rate and personality traits has become a research interest.

In this study, the connection between behaviour and metabolism was examined in the Eurasian perch (*Perca fluviatilis* L.). Also the selectivity of two distinct angling methods was compared in relation to individual behaviour and metabolism. In addition, possible size dependence in capture order was studied. The behavioural trait boldness was used as a measure of personality and was measured in exploratory context as delay time in investigating a new environment. Metabolism was measured as standard metabolic rate (SMR) using fibre optic respirometry. Linear mixed models were used to explain the variation in boldness with individual metabolic rate, angling method, capture order and capture hole.

In this study no association was found between behaviour and standard metabolic rate. Angling method or capture order did not explain the variation in fish behaviour or metabolism. However, boldness was found to be more similar inside capture holes than between capture holes, which was interpreted as reflecting assortativeness within perch shoals, even though possible day-effect could not be ruled out as a confounded explanatory factor. These results and previous studies suggest that perch individuals either conform to the level of boldness of other group members, or are more likely to shoal with individuals which are closer to them in the shy-bold continuum.

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VÄÄTÄINEN, REETTA: Selittääkö perusaineenvaihduntanopeus persoonallisuuden vaihtelua ahvenella (*Perca fluviatilis* L.)?
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Kalastuksen aiheuttamat evolutiiviset vaikutukset kalapopulaatioihin ovat olleet viime vuosina tutkimuksen kohteena niin kaupallisen, kuin vapaa-ajankalastuksenkin näkökulmasta. Koska kalojen elinkierto pohjautuu geneettiseen säätelyyn, kalapopulaatioihin kohdistuva kalastuspaine suuntaa yksilöitä lisääntymään nuorempana ja pienikokoisempana. Todennäköisesti kalastuksen valikoivuus mm. koon tai käyttäytymisen perusteella lisää populaatioihin kohdistuvaa valintapainetta.

Vapaa-ajankalastuksen valikoivuus esimerkiksi pyyntivälineiden valikoivuuden kautta saattaa kohdistua myös kalojen persoonallisuuspiirteisiin, jotka osittaisen geneettisen säätelyn alaisina ovat myös luonnonvalinnan kohteina. Koska erot persoonallisuuspiirteissä on eri eläinryhmillä yhdistetty elinkiertopiirteisiin, kuten kasvunopeus tai jälkeläistuotto, ovat kalastuksen evolutiiviset vaikutukset kalapopulaatioihin myös kalataloudellisesti ja kalastuksen säätelyn kannalta kiinnostavia. Koska myös erot yksilöllisessä aineenvaihduntanopeudessa on yhdistetty eroihin elinkiertopiirteissä, ovat mielenkiinnon kohteiksi nousseet aineenvaihduntanopeuden ja persoonallisuuspiirteiden väliset mahdolliset yhteydet.

Tutkimuksessa selvitettiin käyttäytymisen ja aineenvaihduntanopeuden välistä yhteyttä ahvenella (*Perca fluviatilis* L.). Lisäksi verrattiin kahden eri pyyntimenetelmän valikoivuutta suhteessa yksilölliseen käyttäytymiseen ja aineenvaihduntanopeuteen sekä tutkittiin mahdollista kokoriippuvuutta ahventen pilkkimisjärjestyksessä. Persoonallisuuden mittana tutkimuksessa käytettiin käyttäytymispiirrettä rohkeus, jota mitattiin viiveenä siirtyä tutkimaan uutta ympäristöä, ja aineenvaihduntanopeus mitattiin perusaineenvaihduntanopeutena (SMR) käyttäen valokuituoptiikkaan perustuvaa respirometriaa. Lineaarisia sekamalleja käytettiin selittämään yksilöllisiä eroja ahventen käyttäytymispiirteessä rohkeus niiden yksilöllisellä aineenvaihduntanopeudella sekä pyyntimenetelmällä, pyyntijärjestyksellä ja pyyntiavannolla.

Käyttäytymisen ja perusaineenvaihduntanopeuden välillä ei tutkimuksessa löydetty yhteyttä. Käytetty pyyntimenetelmä tai pyyntijärjestys ei selittänyt eroja kalojen käyttäytymisessä tai aineenvaihduntanopeudessa. Ahventen rohkeusaste havaittiin kuitenkin yhtenäisemmäksi pyyntiavantojen sisällä kuin eri avantojen välillä, minkä tulkittiin kuvastavan epäsatunnaista parvirakennetta ahvenilla, vaikka pyyntipäivää ei voitu sulkea pois mahdollisena selittävänä tekijänä. Nämä tulokset sekä aiempi kirjallisuus viittaavat siihen, että ahvenyksilöt joko pyrkivät rohkeuden suhteen mukautumaan muun parven käyttäytymiseen tai parveutuvat todennäköisemmin sellaisten yksilöiden kanssa, jotka sijoittuvat ujous-rohkeus-akselilla niitä itseään lähelle.

CONTENTS

1 INTRODUCTION

The evolutionary changes in fish populations have been studied widely in recent years in the context of commercial fishing (e.g. Heino & Godø 2002, Jørgensen et al. 2007, Darimont et al. 2009, Stenseth & Dunlop 2009). Because life histories have a genetic basis, the increased mortality caused by fishing shifts the age and size at reproduction towards younger and smaller, respectively (Law & Grey 1989, Heino 1998, Heino & Kaitala 1999). In addition, selective fishing for example by size or behaviour is likely to cause additional selection (Conover & Munch 2002). The main research focus has been on commercial fisheries (Jørgensen et al. 2007), although similar consequences have been suggested to occur also in recreational fisheries in freshwater systems (Cooke & Cowx 2006, Lewin et al. 2006, Biro & Post 2008). The portion of recreational fishing by private persons can be species-specifically, locally and nationally significant, and comparable or even superior to commercial fishing, as shown by the catch amounts in Finland in 2010 (Finnish Game and Fisheries Research Institute 2011).

Personality traits, such as boldness or aggressiveness, are possibly linked with vulnerability to fishing (Lewin et al. 2006, Cooke et al. 2007). As a result, fishing may also be selective with respect to different behavioural traits (Uusi-Heikkilä et al. 2008). Biro and Stamps (2008) suggested that individuals with higher activeness, boldness and aggressiveness in comparison with conspecifics, show higher growth rates and reproductive success, as indicated by research on species across animal taxa. Fishing-induced selection on behavioural traits is consequently of applied interest from the perspective of fisheries management as well (Kuparinen & Merilä 2008). As pointed out by Careau et al. (2008), there is a need for further research also on the possible connection between individual metabolic rates and personality variation and furthermore, for the linkages between these and individual life histories (see also Biro & Stamps 2010).

In this study, the association between metabolism and behaviour was examined by assessing individual standard metabolic rate (SMR) with respect to individual variation in the behavioural trait boldness. Also, two distinct capture methods were compared in relation to individual differences in behaviour and metabolism. Other interests of this study were to examine, whether capture order would explain individual differences in boldness, metabolism or life history traits (here only sex and size were considered). The aim of this research was on its part to increase understanding of the selectivity of recreational fishing in relation to fish

behavioural traits and their possible relationships with fish physiology, and through this try to clarify the evolutionary implications of recreational fishing on freshwater fish populations.

The species used in this study was Eurasian perch (*Perca fluviatilis* L., hereafter perch), a shoaling and day-active fish species (Craig 2000). In Finland, recreational fishers captured 8 000 tonnes of perch in 2010, making it the country's most captured fish species in recreational fisheries (Finnish Game and Fisheries Research Institute 2011). Perch is a familiar species to earlier personality and life-history research (e.g. Heibo et al. 2005, Magnhagen & Staffan 2005, Magnhagen & Bunnefeld 2009, Magnhagen et al. 2012).

2 FISH BEHAVIOUR, METABOLISM AND LIFE HISTORIES

2.1 Fish personality

Personality in fish, and in animal research in general, is defined as the existence of inter-individual behavioural differences, which are stable over time and across situations, i.e. as consistent individual differences (CIDs) in behaviour within populations (Sih et al. 2004a,b, Bell et al. 2013, Carere & Maestripieri 2013). Also the terms temperament, behavioural syndromes (suite of correlated behaviours), coping styles/strategies or predispositions have been used in roughly the same meaning for describing personality in animals (Bell 2007, Bell et al. 2013, Carere & Maestripieri 2013). According to this definition, personality only exists in relation to other members of a population – behavioural type in contrast is a suite of behaviours belonging to an individual (Bell 2007). A behavioural trait (or a personality trait; Gosling 2001), in turn, is a single behavioural trait, such as aggression or boldness, representing the individual's behaviour in any single context (Sih et al. 2004). The repeatability of behaviour is determined by Bell et al. (2009) as the fraction of behavioural variation that is due to differences between individuals in comparison with within-individual variation, from the formula:

$$r = s^2_A / s^2 + s^2_A$$

where s^2_A is the variance among individuals and s^2 the variance within individuals over time.

That is to say, when individuals behave consistently over time and differently from each other, the behaviour is repeatable and behaviours with relatively low intra-individual variance compared with high inter-individual variance are more repeatable (Bell et al. 2009).

A significant genetic influence has been shown for many animal behavioural traits in an increasing number of studies in species across animal taxa, including several in fishes (Van Oers et al. 2005, Van Oers & Sinn 2013). Spatial and temporal variation in the environment (e.g. multiple resources ranging from safe to risky) might in part explain the existence of genetic and phenotypic variation in behaviour within populations (Wilson 1998, Stamps 2007). Also perch has been the subject of behavioural research, and behavioural traits, such as boldness, have earlier been described in the species (e.g. Magnhagen et al. 2012).

2.2 Metabolism in fish

The energy budget of a fish consists of energy inflow as well as energy losses in wastes and metabolism and energy allocation to growth (Adams & Breck 1990). Metabolism usually forms a significant portion of the energy expenditure of fish and can be subdivided into: minimal energetic costs for maintaining basic bodily functions, activity (e.g. swimming, behaviour) and feeding related (digestion, absorption and processing of food) energetic costs (Jobling 1993). Standard metabolic rate (SMR) has been widely used in studies on fishes to determine minimal metabolism (e.g. McCarthy 2000, Virani & Rees 2000, O'Connor et al. 2005, Seppänen et al. 2009a, Maciak & Konarzewski 2010, Voutilainen et al. 2011). SMR is defined as the energy use of a fasting fish at rest, and is normally measured in rate of oxygen consumption at a constant temperature (Adams & Breck 1990), e.g. ml O_2/kg/ h. SMR is measured from fish which are not actively swimming, in a post-absorptive state (Adams & Breck 1990).

The main factors affecting SMR within a species are body size and temperature, so that small fish consume more oxygen per weight unit than large fish and an increase in water temperature increases oxygen consumption (Jobling 1993, Brodte et al. 2006). Also developmental stage (Cunha et al. 2007; Seppänen et al. 2010) and food availability (short- or long-term; Binner et al. 2008) affect standard metabolic rate. The importance of SMR in the energy budget lies in the fact that it sets the limit for the amount of energy available for growth, given constant food intake (Adams & Breck 1990).

Several studies have shown the existence of CIDs in SMR in a wide range of animal taxa (Nespolo & Franco 2007), and also in fishes (e.g. McCarthy 2000, Virani & Rees 2000, Maciak & Konarzewski 2010). The heritability of minimal metabolism has not been widely studied (Biro & Stamps 2010), but research on birds has found evidence for a significant

heritable genetic component in basal metabolic rate (BMR), although this was mostly dependent on that of body mass (Rønning et al. 2007).

2.3 Connections between behaviour, life history and metabolism

As briefly discussed in the introduction, behavioural traits have been shown to be connected to life history traits (Biro & Stamps 2008). In brown trout (*Salmo trutta* L.), a correlation between growth rate and aggressiveness has been reported (Lahti et al. 2001). Variation in the shy-bold continuum may influence individual predation risk, diet and consequently growth (Wilson et al. 1993). In shoaling fish, shoal boldness has been connected to activeness (Harcourt et al. 2009). Westerberg et al. (2004) reported a connection between boldness and higher competitive ability and prey attack order, as well as between competitive ability and growth (Westerberg et al. 2004).

Also metabolism has been found to be connected with life history traits. In fish, metabolic rate (like boldness) has been shown to be connected with growth rate (Yamamoto et al. 1998, Seppänen et al. 2009a) and status (Yamamoto et al. 1998, Metcalfe 1995). For example in Atlantic salmon, growth rate is strongly genetically and phenotypically correlated with the age at smolting, as size determines the onset of smolting (Metcalfe et al. 1998, further discussed in Seppänen et al. 2009a). In salmonids, a positive correlation has been found between the level of metabolism and social status (e.g. Metcalfe et al. 1995, Yamamoto 1998).

Finally, the association between behavioural traits and metabolism is an emerging topic of interest between the research fields of animal physiology and animal personality (Careau et al. 2008, Biro & Stamps 2010). The supporting evidence linking behavioural traits and standard metabolism is at present scarce (Lantová et al. 2011, Seppänen et al. 2009b), but the fact that both of these trait types have been connected with various life history traits (e.g. both have been shown to correlate with growth rate and status), as reviewed above, and that changes in behaviour and metabolism often coappear in some other context [starvation was followed by both lowered SMR and reduced swimming activity in roach (*Rutilus rutilus* L.) and burbot (*Luta luta* L.; Binner et al. 2008)], begs for further research of their possible interactions (Careau et al. 2008, Biro & Stamps 2010). So far, research done in the root vole (*Microtus oeconomus* Pallas; Lantová et al. 2011) and Atlantic salmon (Seppänen 2009b) show little support for the expected correlation between metabolic rate and behavioural traits. Previously, high SMR has been associated with high aggression (Cutts et al. 1998), and Lahti et al. (2002)

have found individual and population level correlations between aggressiveness and SMR in brown trout (*Salmo trutta* L.).

3 RESEARCH HYPOTHESES

The main research hypothesis was that individuals with higher standard metabolic rates would show higher boldness. In addition, it was expected that bolder fish would be captured with the artificial lures as opposed to the natural baits. In relation to capture order, bolder fish with higher metabolism were expected to be captured first. Larger individuals were expected to be captured first in order, since such an observation was made in certain perch populations in a previous study (Vainikka et al. 2012).

4 MATERIALS AND METHODS

4.1 Study fish

The perch used in this study were captured from Lake Pohjalampi (62◦40′ N, 29◦33′ E) in Liperi, Eastern Finland. Lake Pohjalampi is a small and shallow mesotrophic lake with a surface area of 0.61km^2, an average depth of 3.2 m and a maximum depth of 5.3 m (Leppä et al. 2003). The lake has experienced algal blooms and hypolimnetic wintertime oxygen depletion in the 80's and 90's and has been subjected to cyprinid removals during 1993-97 (Karjalainen et al. 1999, Tolonen et al. 2000, Leppä et al. 2003). Based on test fishings performed in 2000 the major fish species were roach (*Rutilus rutilus* L.) and perch, accompanied by ruffe (*Gymnocephalus cernuus* L.) and pike (*Esox lucius* L.) (Leppä et al. 2003).

The perch for this study (n=82) were captured by ice fishing between 9 a.m. and 3 p.m. on three occasions: on 6th (n=40) and 14th (n=12) of February and on 21st of March (n=30) 2013. The ice-fishing locations were chosen by drilling holes along the littoral slopes of the lake until a perch shoal was encountered (method further described in Vainikka et al. 2012). The holes were at least 5 metres apart and each hole was angled until no fish were caught for 1 minute. The perch were captured using two commonly used ice fishing methods: an artificial lure (coloured triple hook) or a natural bait (2-4 live bloodworms i.e. Chironomidae larvae placed on a simple mormyshka hook), and only one method was used per hole. The artificial lure comprised of an upright lure (ViM Pirken 34 mm, 4 g) and a coloured triplehook (Red Lime #14, ViM Pirken) used with a simple rigid ice-fishing rod (VM Pimpelspö) and

0.16 mm fishing line (Stroft GTM, Germany). With the mormyshka hook, a sensitive-tipped rod with 0.10 mm fishing line (Trabucco Super Elite T1 Tournament, Italy) was used.

The aim of the use of two distinct methods was to capture individuals with distinguishable personalities, assuming that the artificial lure would attract bolder or less neophobic individuals towards novel food items, as opposed to the natural bait (Magnhagen & Staffan 2003). Both capture methods were used on each capture date and in every location, in order to account for any day-effect and spatial variation in the results.

Following each capture, the perch were anaesthetized in a 10 l bucket using clove oil mixed with ethanol (1:9) and water for a clove oil content of 60 mg/l (Hoskonen & Pirhonen 2003). The perch were marked under anaesthesia with passive integrated transponders (7 × 1.35 mm FDX-B PIT tag, Loligo® Systems, Tjele, Denmark), inserted under the skin next to the dorsal fin. The perch were placed in a 50 l cool box and transferred to laboratory of the University of Eastern Finland, Joensuu campus, where they were kept and tested in 8°C tap water and were offered freeze-dried bloodworms or flakes once a week. Light rhythm was set to 12 hours from 7 a.m. to 7 p.m.

4.2 Metabolic rate

Metabolic rates of the perch were measured before the behavioural trials, as suggested advisable by previous work (Biro & Stamps 2010). Oxygen consumption was measured at 8°C using automated intermittent respirometry (DAQ-PAC-F4, Loligo® Systems) with fibre optic sensors. Three parallel transparent acrylic chambers with volumes of 295-297 ml, or 825-830 ml, for fish with a body mass greater than 23 g, were used. Fish body mass was measured as wet weight prior to respirometry. Flow rate was set to approximately one chamber volume/min. Photoperiod was 12L:12D, and respirometry was usually started soon after 8 a.m. The perch had been fasted for 48 h and temperature acclimated for a minimum of 4 days before respirometry. Oxygen consumption was measured over a 24 hour period, using a 25 minute loop with 5 and 10 minute flush and wait periods, respectively, followed by a 10 minute measuring period. The data from the respirometry were saved by AutoResp-software (Loligo® Systems) once every second.

Oxygen consumption was calculated from the slope of the oxygen depletion (% air saturation/h) during a measuring period. Using r^2-fitting on an 80% span for each slope, from seven loops with lowest oxygen consumption levels, the average of five highest was used to calculate SMR (mg O_2/kg/h). As pointed out by Voutilainen et al. (2011), it is a common

practice to use an average of at least two of the lowest oxygen consumption values, due to possible non-linear decrease in the partial pressure of O_2 during measurement, and furthermore because metabolism may be affected by small changes in body temperature and hormone levels, and thus is not constant even at rest (Voutilainen et al. 2011).

Only measuring periods with a slope r^2-value greater than 0.7 were accepted, and from the 24-hour data, only the chambers with at least 25 (up to 90) accepted loops (slopes) were used. Microbial respiration was measured from empty chambers before and after the measurements of each fish, and the average of these was subtracted from the total oxygen consumption of each chamber. In the computerized r^2-fitting process, two additional loops with lowest O_2-consumption values were left out to ensure that no extra loops with empty chambers were mistaken for those of the perch. From the total oxygen consumption data, the mass-specific SMR was calculated from the formula:

$$SMR = (DO \times V_{chamber} / SO_2) \times (m - m_{bact}) / FM$$

where DO=amount of dissolved oxygen in ambient water (mg/l), $V_{chamber}$=chamber volume (l), SO_2=air saturation (100%/h), m=decline in amount of O_2 (% air saturation/h), m_{bact}=bacterial respiration (% air saturation/h) and FM=fish mass (kg).

15 perch were measured twice for oxygen consumption levels within 6 to 32 days, in order to estimate the repeatability of SMR. Size-dependence was accounted for by using the residuals from linear regression (in Excel 2010, Microsoft, USA) of $\log_{10}$-transformed SMR (mg O_2/h) on $\log_{10}$-transformed wet weight (g) as a measure of metabolic rate (Metcalfe et al. 1995, McCarthy et al. 2000, Seppänen et al. 2009a). The residual values (relative SMR or rSMR) were positive for fish with higher SMR than expected from body mass, and conversely negative for fish with lower SMR than expected (Metcalfe et al. 1995). To see, whether the acclimation of the perch to the shift in temperature between the lake and the laboratory caused any bias on the SMR results, correlation was looked for between rSMR and the time between capture date and respirometry. Respirometric data from the individuals that died before the end of all the experiments were not used in any analyses, although no abnormal patterns in SMR were found in these perch.

4.3 Behavioural tests

To assess personality, a test for boldness (exploratory behaviour) was carried out using a plastic box (arena, 760×360×200 mm, with outflow holes at 80 mm) holding 22 litres of

water. At one end of the arena, there was a start box (150×150 mm), separated by a hatch, where each perch was placed for a five-minute acclimation prior to the behavioural trial. At the opposite end there was a mirror (360x80 mm), midway was indicated by a marker line and between the midway and the starting box there was a plastic plant with a small rock on each side acting as potential shelter. The trials were conducted under dim lighting with an infrared light and a web camera placed over the arena. The time until each behavioural event of the fish (time out of start-box; time to shelter; time to midway; time to mirror) was recorded with a computer using AV Bio- Statistics software (v. 4.9, by A. Vainikka).

The experiment measures the delay time to investigate a novel environment, i.e. boldness in exploratory context. This kind of an experiment is commonly used in fish behaviour research to measure boldness (Budaev & Brown 2011). The duration of the trials was 30 minutes, except for perch which reached the mirror at time point 20 minutes or after, in which case the trial was ended when the mirror was reached. The trials took place between 9 a.m. and 15 p.m. The experiment was done twice for each perch with a minimum of 1 (and up to 18) night(s) between the trials. To see, whether the amount of days spent in the laboratory before the boldness trials affected the results of the trials, correlation was looked for between the boldness score from the first trial and the amount of days between capture and the first boldness trial.

After the behavioural experiments, blood samples were taken from the perch for later hormonal analysis, weight and length were measured and sex determined. Operculums and scale samples were collected for later age determination, not described here. This study was licensed by the National Animal Experiment Board (license number ESAVI/1906/04.10.03/2012).

4.5 Statistical methods

Repeatabilities of SMR, body mass (as requested by Maciak and Konarzewski 2010) and behaviour were evaluated using the intraclass correlation coefficient (Lessells & Boag 1987, MacCarthy 2000) using AV Bio-Statistics. Data preparations were performed in Excel and all subsequent statistical tests were performed in SPSS for Windows (v. 19, IBM, USA). Kolmogorow-Smirnov Z-test and a histogram-based estimation were used to assess the normality of the data. Length, weight and rSMR values were normally distributed and logarithmic transformation was used for the behavioural time variables (lnOut, lnShelter, lnMidway, lnMirror). All correlations were estimated using Pearson's product moment

correlation coefficient. Using principal component analysis (PCA), the behavioural time variables were reduced into a single component. Since the original factor scores derived from the principal component analysis were higher for higher time values in the behavioural trials, their opposite (multiplied with -1) numbers were used to represent boldness (boldness score). Thus, individuals with faster emergence and activity times had a higher boldness score value to represent their higher boldness in the trials and vice versa. To assess the change in the repeatability of boldness as a function of time, the differences between the repeated individual boldness estimates were plotted against the time between the behavioural trials.

A linear mixed-effects model was designed to explain the variability in the response variable boldness. The predictor variables used in the model were as follows: capture hole, used lure type and sex as categorical variables, and relative SMR, capture order, length and body mass as continuous variables. A random intercept was included as a random factor along with the effect of individuals (PIT number) as subject. Repeat time (of the boldness trials, repeat 1 and 2) was set as a repeated variable. A hierarchical nested design was used in the model, where the term capture hole was nested within the term lure type, since only one lure type was used per hole. The term capture order was further nested within the two previous, since capture order per each hole was dependent on capture hole and consequently on the lure type that was used for that hole.

The fit of the model was assessed using Akaike's information Criterion (AIC). All variables were included in the original model, and were subsequently removed one by one, in order of least significance, until the best fitting model was reached. In the final model, only the nested predictor variables capture hole and lure type were maintained.

In addition, a general linear model was used in explaining the variability in rSMR with again, the nested terms lure type, capture hole and capture order. Also sex as a categorical variable was included in the first version of the model. A general linear model with nested terms (see above) was used also to explain capture order by size. When determining possible sex-dependence, immature perch (n=3) were excluded from the models.

5 RESULTS

Out of 82 in total, 40 perch were caught using the artificial lure and 42 using the natural bait from 28 capture holes, with an average of 3 perch per hole (S.D. 3.2, range 1-12). Behaviour was found to be repeatable (table 1). The perch left the start box in 57% of all the behavioural trials (n=102) and 22% (11 out of 51 perch) did not leave the start box in either of the trials.

PCA on the behavioural time variables was performed based on the Kaiser-Meyer-Olkin Measure of Sampling Adequacy (KMO=0.786) and Bartlett's test of Sphericity ($p<0.001$). The principal component extracted from the PCA explained 91.4% of the variation in the behavioural time variables (table 1).

Table 1. Repeatability of behavioural time variables (trials n=102 on 51 individuals) and results from PCA. The number of trials in which the maximum time of 30 minutes was reached on a variable (i.e. no activity for the variable) is reported as # max. PCA factor loadings, eigenvalue and fraction of behavioural variance explained by the principal component are shown as well as repeatability of boldness scores based on the factor score from PCA for trial 1 and 2.

Variable	r	p	# max	PCA
Time to emerge	0.26	< 0.05	44	0.896
Time to shelter	0.34	< 0.01	50	0.974
Time to midway	0.46	< 0.001	54	0.976
Time to mirror	0.45	< 0.001	54	0.976
Eigenvalue				3.657
% of variance explained				91.43
Boldness score	0.42	< 0.001		

The repeatability (r=0.42) of the boldness scores of the two behavioural trials was highly significant (table 1). (If the perch that did not leave the start box in either trial were excluded, r=0.32, $p<0.05$, n=40). No correlation (r=0.06, p=0.69) was found between the number of days between the trials and the difference between the boldness score from trial 1 and 2 (fig. 1).There was a slight but non-significant positive correlation (r=0.26, p=0.07, n=51) between the boldness score and the amount of days between capture and the first boldness trial.

Oxygen consumption rate (mg/h) was correlated with fish weight (r=0.87, $p<0.001$, n=51). The mass-specific SMR values varied between 23.65 and 57.76 mg O_2/kg/h (table 2). Mass-specific SMR was repeatable, as well as body mass (table 2). No correlation (r=0.11, p=0.45, n=51) was found between rSMR and the time between capture date and respirometry.

From the factors added to the mixed model, only capture hole explained variation in boldness (table 3) and the effect was highly significant (p=0.001). To see whether capture hole depth would account for this result, the average of all boldness scores for each capture hole with more than 3 perch caught from them was compared with corresponding capture hole depth. No significant correlation was found (r=0.64, p=0.09, n=8).

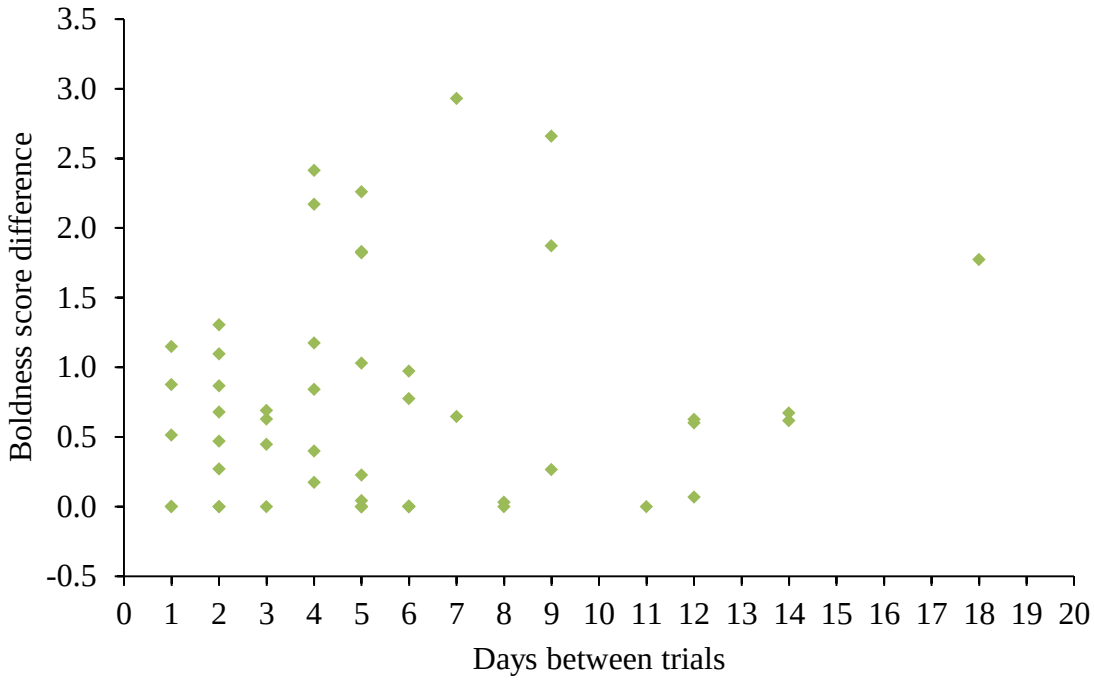

Figure 1. Days between trials versus boldness score difference (n=51). The x-axis represents the number of days between the two boldness trials and the y-axis the difference between the boldness scores from trials 1 and 2 for each perch (#min=11). No regression line could feasibly explain any trend in the scatter.

Table 2. Means and standard deviations for length (L), mass (M) and mass-specific SMR of the perch (n=51). Repeatabilities of body mass and SMR are shown (n=15), as well as the linear regression equation for the $\log_{10}$–transformed variables y=SMR (mg/h) and x=body mass (g) and corresponding r^2-value.

	Min	Max	Mean ± SD	r	p
L (mm)	111	201	155 ± 21.8		
M (g)	13.1	91.0	37.5 ± 17.4	0.98	>0.001
SMR mg O_2/kg/h	23.7	57.8	36.5 ± 7.5	0.75	>0.001
Linear regression equation	y=0.8881x - 1.2746		r^2=0.823		

Table 3. Results from the mixed model, in which boldness score was set as response variable (n=51). The fixed effects and their significance levels are shown.

Variable	df	F	p
rSMR	1	0.35	0.56
Lure type	1	0.10	0.75
Capture hole (Lure type)	15	3.63	0.001
Capture order (Capture hole(Lure type))	29	0.42	0.53
Intercept	1	0.24	0.63
Sex (n=48)	1	0.14	0.71

Relative SMR or lure type did not explain variation in boldness (fig. 2), nor did capture order or sex (table 3). Based on the general linear model, capture hole, capture order, lure type or sex did not explain the variation in rSMR (table 4). Perch size was not explained by capture order (F=1.384, df=1, p=0.245, n=66, fig. 3).

Table 4. Results from the general linear model. The response variable was rSMR (n=51). The fixed effects and significance levels are shown.

Variable	df	F	p
Lure type	1	0.34	0.57
Capture hole (Lure type)	5	0.98	0.45
Capture order (Capture hole(Lure type))	7	1.11	0.40
Sex (n=48)	1	1.43	0.26

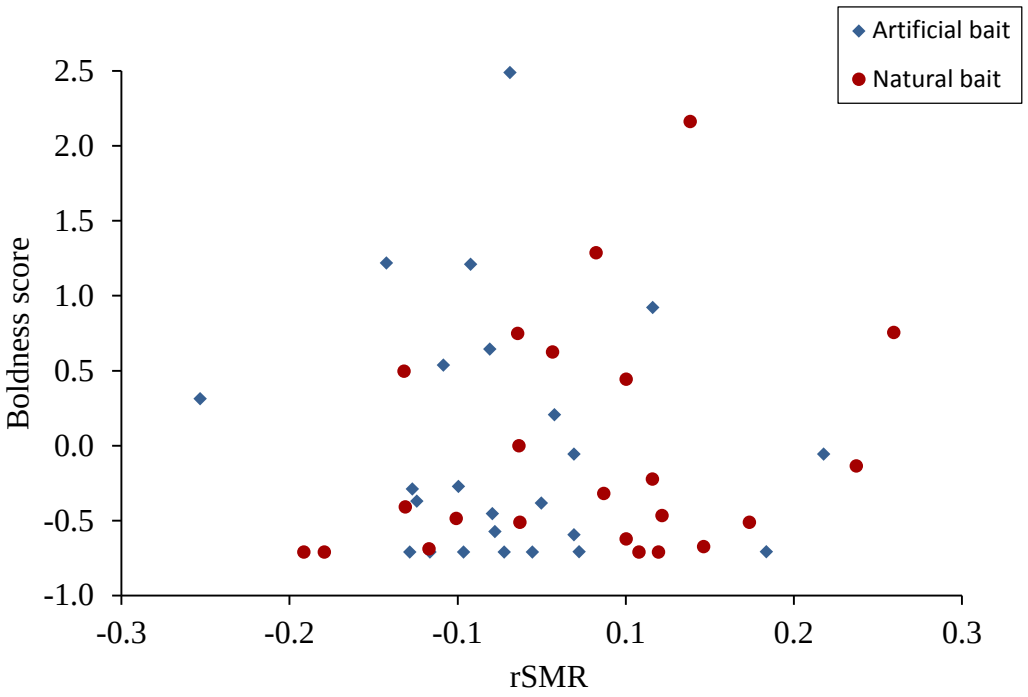

Figure 2. Average of the boldness scores from the two behavioural trials plotted against relative SMR (n=51). Blue rhombuses represent perch captured with the artificial bait and red circles perch captured with the natural bait.

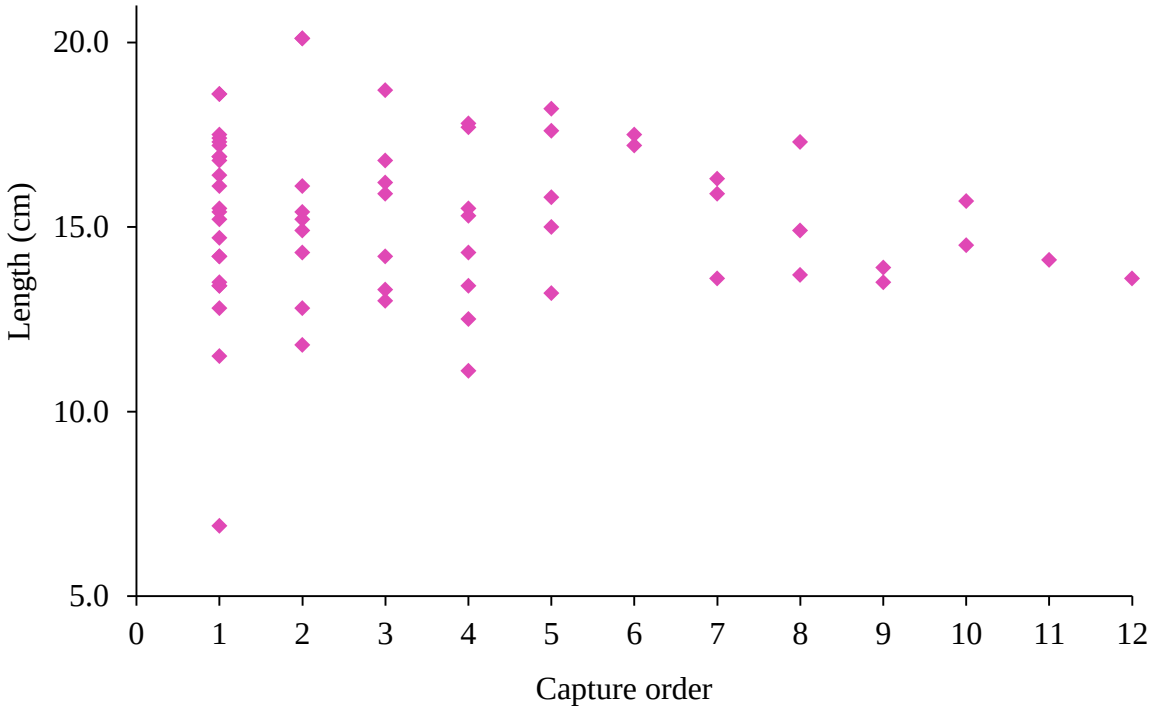

Figure 3. Perch length (cm) plotted against capture order (n=66).

6 DISCUSSION

The perch in this study showed significantly repeatable behaviour, suggesting that consistent individual differences in behaviour, i.e. personality, are potentially significant both ecologically and evolutionarily in this species. According to this study, standard metabolic rate (rSMR) did not explain variation in the boldness of the perch (table 3, fig. 2). The results did not support the predictions of positive correlation between individual behaviour, metabolism and vulnerability to angling with artificial gear (Lewin et al. 2006, Cooke et al. 2007, Careau et al. 2009, Biro & Stamps 2010). No association between the capture order and fish size was found either. However, past growth rate or hormonal factors were not yet included in this thesis. It is therefore possible that personality variation could be explained by variation in other physiological or life-history traits rather than metabolism, and such associations remain to be explored by future studies.

Because all the perch used in this study were susceptible to angling, it would most likely increase behavioural and metabolic variation, if the non-susceptible individuals (the ones who did not take the bait) could be included in the tests. This would result in a more accurate general picture of the connection between SMR and behaviour. Of interest would also be comparing the rSMR and boldness values of this study to individual life history traits (growth variable) and stress- and metabolic hormone levels, which will be done in the future.

No association between lure type and level of boldness was found. However, in another study using similar lure types, Härkonen et al. (2013, unpublished) found that perch captured with the artificial lure showed higher short-term exploratory behaviour, whereas perch captured with the natural bait showed higher long-term boldness in space use after habituation to predation risk in a group test in semi natural environment. The different result might be due to different experimental settings: here, no separation was made between short- and long-term boldness and only two individual tests were performed in laboratory environment. In contrast, Härkönen et al. used outdoor settings and automated measurements while the perch were in shoals, which might have resulted in a more natural behavioural response in the perch. However, individually assessed behaviour is known to predict behaviour in comparable group setting in perch (Kekäläinen et al. 2013, unpublished)

In a previous study (Vainikka et al. 2012), perch size slightly decreased with respect to capture order in two out of ten tested populations, which was interpreted by the authors as being due to possible size-dependent hierarchy in eating order in perch. This study, however, showed no such correlation between capture order and size (fig. 3). This could be due to the highly variable numbers of perch captured per each hole or the sampling method in which the time interval between captured fish was longer than in the other study. In Vainikka et al. (2012) the fish were killed immediately after capture, whereas in this study the perch were anaesthetized and tagged before proceeding with the ice fishing.

The repeatability of SMR found in this study (r=0.75) was consistent with earlier studies with fish, where similar repeatabilities in SMR [r=0.68 of McCarthy 2000, rSMR for Atlantic salmon; r=0.68 of Virani & Rees 2000, SMR for the Gulf killifish (*Fundulus grandis* Baird & Girard) and r=0.68 of Maciak & Konarzewski 2010, rSMR for the spined loach (*Cobitis taenia* L.); also reviewed across animal taxa in Nespolo & Franco 2007] have been observed.

As found in Atlantic salmon by O'Connor et al. (2005), rSMR can be affected by starvation (duration 1 month in the study). In the study, the salmon were subjected to food deprivation and as a result, the rank order of rSMR between the individuals broke down and subsequently returned to previous state once food was re-introduced. Eurasian perch has been shown to suffer from food deprivation during winter, caused most likely by low light levels (Eckmann 2004), but seasonal or food deprivation -induced changes in perch SMR have not been studied. Therefore it remains unclear whether food deprivation changes the rank order in rSMR in perch as it does in Atlantic salmon (O'Connor 2005), but it would be worth considering in future studies.

No correlation was found between rSMR and the time between capture date and respirometry, showing that no clear bias to the results was caused by the acclimation of the perch to the shift in temperature between the lake and the laboratory.

The repeatability of behaviour found in this study ($r=0.42$, $p<0.001$, table 1) matched those found in previous studies: the average repeatability of different behavioural traits across animal taxa was $r=0.37$ (Bell et al. 2009). The lack of correlation between the number of days between the trials and the difference between the boldness score from the two trials (fig. 1) suggests that the time passed from previous experience did not strongly affect the results of the second trial.

The most interesting result in the study was that capture hole explained differences in behaviour. In reality, the capture hole -effect most likely represents perch shoals (as it is reasonable that different shoals were angled from different holes), and therefore the results suggest that the perch were more similar in boldness within shoals than between shoals. This result is consistent with the findings of Magnhagen and Staffan (2005) in young-of-the-year perch, according to which at least one measure of boldness (time spent in the open) was to some extent influenced by other members of the group. Similarly, Magnhagen and Bunnefeld (2009) showed that the boldness of perch within groups was mainly influenced by the boldness of the other members of the group, and Dyer et al. (2009) found that group composition in terms of boldness levels influenced the behaviour of individual guppies (*Poecilia reticulata* Peters).

A study on three-spined sticklebacks (*Gasterosteus aculeatus* L.) showed that groups would modify their activity levels according to the boldness level of a fish entering the shoal (Harcourt et al. 2009). However, the same study on sticklebacks suggested that regardless of the focal individuals' own phenotype, they would prefer associating more time overall with bolder and more active shoals, rather than shy ones (Harcourt et al. 2009) – even though shy hungry fish spent more time with a shy shoal than shy fed fish – which was interpreted as an effort to reduce inter-individual competition (Harcourt et al. 2009).

Overall, the results of this study once more raise the question of the role of other group members on individual behaviour in shoaling fish species (Magnhagen 2012) and the subject should be further investigated in social context as opposed to only individual testing used here. This is also supported by the results of Magnhagen & Staffan (2009), who found that perch show shyer behaviour when alone than in groups, and that this effect was stronger in relatively shyer individuals as opposed to bolder ones.

However, the results found here on intragroup behavioural similarity as opposed to that of between groups, would best be verified with another dataset, since here only 8 out of 28 capture holes had more than 3 perch captured from them. These holes were used in 3 separate days, so a possible day-effect could not be ruled out as a source of variation in boldness. However, there was no significant correlation between the boldness score and the amount of days between capture and the first boldness trial, suggesting that the amount of time spent in the laboratory before the behavioural trials did not significantly bias the results of the trials. Capture depth was not found to significantly account for the average boldness between different capture holes. However, again, only 8 capture holes had more than 3 perch captured from them, and a higher capture hole number might show a significant correlation between capture depth and boldness. The capture method used here did not allow for the separation of capture hole and capture hole depth, so the connection between capture depth and perch boldness should be studied elsewhere.

Out of 82 perch captured, 1 died after transportation and 11 (13%) were put down or died in the laboratory before the end of all the tests. All these fish were caught on the first two capture dates (7 and 4, respectively), suggesting that prolonged stress from unnatural environment might be at least a partial source for the captive mortality, as perch are known to be highly sensitive to stress (Douxfils et al. 2011).

7 CONCLUSIONS

This study found no correlation between the consistent individual differences in boldness and standard metabolic rate in Eurasian perch. In addition, factors such as used lure type or capture order did not explain for the individual differences in behaviour or metabolism. Perch size was not found to predict capture order. However, capture hole explained differences in boldness, which was interpreted as being due to group compositions, in which individuals are more alike in their level of boldness within groups than between groups. Capture depth did not account for the boldness differences between capture holes, but day-effect could not be ruled out as an explanatory factor.

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REFERENCES

Adams, S.M., Breck, J.E. 1990: Bioenergetics. – In: Schreck, C.B. & Moyle, P.B. (ed.), Methods for fish biology: 389-415. American Fisheries Society. Maryland.

Bell, A.M. 2007: Future directions in behavioural syndromes research. – Proceedings of the Royal Society B: Biological Sciences 274: 755-761.

Bell, A.M., Hankison, S.J., Laskowski, K.L. 2009: The repeatability of behaviour: a meta-analysis. – Animal Behaviour 77: 771-783.

Bell, A.M., Foster, S.A., Wund, M. 2013: Personality in stickleback fish. – In: Carere, C. & Maestripieri, D. (ed.), Animal personalities: Behavior, Physiology, and Evolution: 36-65. The University of Chicago Press, Chicago.

Binner, M., Kloas, W., Hardewig, I. 2008: Energy allocation in juvenile roach and burbot under different temperature and feeding regimes. – Fish Physiology and Biochemistry 34:103-116.

Biro, P., Post, J. 2008: Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. – Proceedings of the National Academy of Sciences 105: 2919-2922.

Biro, P., Stamps, J.A. 2008: Are animal personality traits linked to life-history productivity? – Trends in Ecology & Evolution 23: 361-368.

Biro, P., Stamps, J.A. 2010: Do consistent individual differences in metabolic rate promote consistent individual differences in behaviour? – Trends in Ecology & Evolution 25: 653- 659.

Brødte, E., Knust, R., Pörtner, H.O. 2008: Temperature-dependent energy allocation to growth in Antarctic and boreal eelpout (Zoarcidae). – Polar Biology 30: 95-107.

Budaev, S. & Brown, C. 2011: Chapter 7: Personality traits and behaviour. – In: Brown, C., Laland, K. & Krause, J. (ed.), Fish Cognition and Behavior, Second Edition: 135-165. Wiley-Blackwell. Oxford.

Careau, V., Thomas, M., Humphries, M., Réale, D. 2008: Energy metabolism and animal personality. – Oikos 117: 641-653.

Carere, C., Maestripieri, D. 2013: Introduction: Animal personalities: Who cares and why? – In: Carere, C. & Maestripieri, D. (ed.), 2013: Animal personalities: 1-9. The University of Chicago Press. Chicago.

Cooke, S.J., Cowx, I.G. 2006: Contrasting recreational and commercial fishing: Searching for common issues to promote unified conservation of fisheries resources and aquatic environments. – Biological Conservation 128: 93-108.

Cooke, S.J., Suski, C.D., Ostrand, K.G., Wahl, D.H., Philipp, D.P. 2007: Physiological and behavioral consequences of long-term artificial selection for vulnerability to recreational angling in a teleost fish. – Physiological and Biochemical Zoology 80: 480-90.

Conover, D.O., Munch, S.B. 2002: Sustaining fisheries yields over evolutionary time scales. – Science 297: 94–96.

Craig, J.F. 2000: Percid fishes: Systematics, Ecology and Exploitation. – 370 pp. Wiley-Blackwell. Oxford.

Cutts, C.J., Metcalfe, N.B., Taylor, A.C. 1998: Aggression and growth depression in juvenile Atlantic salmon: the consequences of individual variation in standard metabolic rate. – Journal of Fish Biology 52: 1026-1037.

Darimont, C.T., Carlson, S.M., Kinnison, M.T., Paquet, P.C., Reimchen, T.E., Wilmers, C.C. 2009: Human predators outspace other agents of trait change in the wild. – Proceedings of the National Academy of Sciences 106: 952-954.

Douxfils, J., Mandiki, S.N.M., Marotte, G., Wang, N., Silvestre, F., Milla, S., Henrotte, E., Vandecan, M., Rougeot, C., Mélard C., Kestemont P. 2011: Does domestication process affect stress response in juvenile Eurasian perch *Perca fluviatilis*? – Comparative Biochemistry and Physiology, Part A 159: 92-99.

Dyer, J.R.G., Croft, D.B., Morrell, L.J., Krause J. 2009: Shoal composition determines foraging success in the guppy. – Behavioral Ecology 20:165-171.

Finnish Game and Fisheries Research Institute 2011: Fisheries and hunting statistics. http://www.rktl.fi/english/statistics. 20.8.2013.

Gosling, S.D. 2001: From mice to men: what can we learn about personality from animal research? – Physiological Bulletin 127: 45-86.

Harcourt, J.L., Sweetman, G., Johnstone, R.A., Manica, A. 2009: Personality counts: the effect of boldness on shoal choice in three-spined sticklebacks. – Animal Behaviour 77: 501-1505

Heibo, E., Magnhagen, C., Vollestad, L.A. 2005: Latitudinal variation in life-history traits in Eurasian perch. – Ecology 86: 3377-3386.

Heino, M., Godø, O.R. 2002: Fisheries-induced selection pressures in the context of sustainable fisheries. – Bulletin of Marine Sciences and Fisheries 70: 639-656.

Heino, M. 1998: Management of evolving fish stocks. – Canadian Journal of Fisheries and Aquatic Sciences 55: 1971-1982.

Heino, M., Kaitala, V. 1999: Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. – Journal of Evolutionary Biology 12: 423-429.

Hoskonen, P., Pirhonen, J. 2003: Neilikkaöljy – uusi vaihtoehto kalojen nukutukseen. http://users.jyu.fi/~jpirhon/nukuttaminen.pdf. 20.8.2013.

Jobling, M. 1993: Bioenergetics: feed intake and energy partitioning. – In: Rankin, J.C. & Jensen, F.B. (ed.), Fish Ecophysiology: 1-44. Chapman & Hall. Suffolk.

Jørgensen, C., Enberg, K., Dunlop, E.S., Arlinghaus, R., Boukal, D.S., Brander, K., Ernande, B., Gårdmark, A., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M., Rijnsdorp, A.D. 2007: Managing evolving fish stocks. – Science 318: 1247-1248.

Karjalainen, J., Leppä, M., Rahkola, M., Tolonen, K. 1999: The role of benthivorous and planktivorous fish in a mesotrophic lake ecosystem. – Hydrobiologia 408/409: 73-84.

Kuparinen, A., Merilä, J. 2008: Detecting and managing fisheries-induced evolution. –Trends in Ecology & Evolution 22: 652-659.

Lantová, P., Zub, K., Koskela, E., Šíchová, K., Borowski, Z. 2011: Is there a linkage between metabolism and personality in small mammals? The root vole (*Microtus oeconomus*) example. – Physiology & Behavior 104: 378-383.

Lahti, K., Laurila, A., Enberg, K., Piironen, J. 2001: Variation in aggressive behaviour and growth rate between populations and migratory forms in the brown trout, *Salmo trutta*. – Animal Behaviour 62: 35-44.

Lahti, K., Huuskonen, H., Laurila, A., Piironen, J. 2002: Metabolic rate and aggressiveness between brown trout populations. – Functional Ecology 16: 167-174.

Law, R., Grey, D.R.1989: Evolution of yields from populations with age-specific cropping. – Evolutionary Ecology 3: 343–359.

Leppä, M., Hämäläinen, H., Karjalainen, J. 2003: The response of benthic macroinvertebrates to whole-lake biomanipulation. – Hydrobiologia 498: 97-105.
Lessels C.M., Boag, P.T. 1986: Unrepeatable repeatabilities: a common mistake. – The Auk 104: 116-121.
Lewin, W.-C., Arlinghaus, R., Mehner, T. 2006: Documented and potential biological impacts of recreational fishing: Insights for management and conservation. – Reviews in Fisheries Science 14: 305-367.
Maciak, S., Konarzewski, M. 2010: Repeatability of standard metabolic rate (SMR) in a small fish, the spined loach (*Cobitis taenia*). – Comparative Biochemistry and Physiology, Part A 157: 136-141.
McCarthy, I.D. 2000: Temporal repeatability of relative standard metabolic rate in juvenile Atlantic salmon and its relation to life history variation. – Journal of Fish Biology 57: 224-238.
Magnhagen, C., Bunnefeld, N. 2009: Express your personality or go along with the group: what determines the behaviour of shoaling perch? – Proceedings of the Royal Society B: Biological Sciences 276: 3369-3375
Magnhagen, C., Staffan, F. 2003: Social learning in young-of-the-year perch encountering a novel food type. – Journal of Fish Biology 63:824–829.
Magnhagen, C., Staffan, F. 2005: Is boldness affected by group composition in young-of-the-year perch (*Perca fluviatilis*)? – Behavioral Ecology and Sociobiology 57: 295-303.
Metcalfe, N.B., Taylor, A.C., Thorpe, J.E. 1995: Metabolic rate, social status and life-history strategies in Atlantic salmon. – Animal Behaviour 49: 431-436.
Metcalfe, N.B., Huntingford, F.A., Graham, W.D., Thorpe, J.E. 1998: Early social-status and the development of life-history strategies in Atlantic salmon. – Proceedings Of The Royal Society B: Biological Sciences 236: 7-19.
Nespolo, R.F., Franco, M. 2007: Whole-animal metabolic rate is a repeatable trait: a meta-analysis. – The Journal of Experimental Biology 210: 2000-2005.
O'Connor, K.I., Taylor, A.C., Metcalfe, N.B. 2005: The stability of standard metabolic rate during a period of food deprivation in juvenile Atlantic salmon. – Journal of Fish Biology 57: 41-51.
Rønning, B., Jensen, H., Moe, B., Bech, C. 2007: Basal metabolic rate: heritability and genetic correlations with morphological traits in the zebra finch. – Journal of Evolutionary Biology 20: 1815-1822.
Seppänen, E., Piironen, J., Huuskonen, H. 2009a: Standard metabolic rate, growth rate and smolting of the juveniles in three Atlantic salmon stocks. – Boreal Environment Research 14: 369-382.
Seppänen, E., Tiira, K., Huuskonen, H., Piironen, J. 2009b: Metabolic rate, growth and aggressiveness in three Atlantic salmon *Salmo salar* populations. – Journal of Fish Biology 74: 562-575.
Seppänen, E., Piironen, J., Huuskonen, H. 2010: Consistency of standard metabolic rate in relation to life history strategy of juvenile Atlantic salmon *Salmo salar*. – Comparative Biochemistry and Physiology, Part A 156: 278-284.
Sih, A., Bell, A., Johnson, J.C. 2004a: Behavioral syndromes: an ecological and evolutionary overview. – Trends in Ecology & Evolution 19: 372-378.
Sih, A., Bell, A., Johnson, J.C., Ziemba, R.E. 2004b: Behavioral syndromes: an integrative overview. – The Quarterly Review of Biology 79: 241-277.
Stamps, J.A. 2007: Growth-mortality tradeoffs and 'personality traits' in animals. – Ecology Letters 10: 355-363.
Stenseth, N.C., Dunlop, E.S. 2009: Unnatural selection. – Nature 457: 803-804.
Tolonen, K.T., Karjalainen, J., Staff, S., Leppä, M. 2000: Individual and population-level food

consumption by cyprinids and percids in a mesotrophic lake. – Ecology of Freshwater Fish 9: 153-162.
Uusi-Heikkilä, S., Wolter, C., Klefoth, T., Arlinghaus, R. 2008: A behavioral perspective on fishing-induced evolution. – Trends in Ecology & Evolution 23: 419-421.
Van Oers, K., Sinn, D.L. 2013: Quantitative and Molecular Genetics of Animal Personality. – In: Carere, C. & Maestripieri, D. (ed.), Animal personalities: behavior, physiology, and evolution: 149-200. The University of Chicago Press. Chicago.
Van Oers, K., de Jong, G., van Noordwijk, A.J., Kempenaers B., Drent, P.J. 2005: Contribution of genetics to the study of animal personalities: a review of case studies. – Behaviour 142: 1191-1212.
Vainikka, A., Koskimäki, J., Niemelä, P., Kortet, R. 2012: Composition of the Eurasian perch (Perca fluviatilis) catches in ice fishing: Does capture order predict body size? – Fisheries Research 115: 24-30.
Virani, N.A., Rees B.B. 2000: Oxygen consumption, blood lactate and inter-individual variation in the gulf killifish, *Fundulus grandis*, during hypoxia and recovery. – Comparative Biochemistry and Physiology, Part A 126: 397-405.
Westerberg, M., Staffan, F., Magnhagen, C. 2004: Influence of predation risk on individual competitive ability and growth in Eurasian perch, *Perca fluviatilis*. – Animal Behaviour 67: 273-279.
Wilson, D.S., Coleman, K., Clark, A.B., Biederman, L. 1993: Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*) – an ecological study of a psychological trait. – Journal Of Comparative Psychology 107: 250-260.
Yamamoto, T., Ueda, H., Higashi, S. 1998: Correlation among dominance status, metabolic rate and otolith size in masu salmon. – Journal of Fish Biology 52: 281-290.